

THE EFFECT OF TEMPERATURE ON THE RIGHTING OF ECHINODERMS

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The righting response of echinoderms has engaged the attention of investigators since Romanes and Preyer first studied it in the eighties of the last century, but the interest lay, in most cases, in analyzing the activities of the nervous system, as they manifested themselves in the reaction to a change in the position of the body. The representatives of the phylum usually employed were the sea-urchin (Echinoidea), the starfish or sea-star (Asteroidea), and the brittle-star (Ophiuroidea), none of which possesses statocysts so important in the righting of higher animals. The sea-urchin and the starfish turn over by the action of their tube-feet, while the brittle-star, which has no tube-feet, depends entirely on the muscular action of its arms.

Jennings (1907), in his extended report on the behavior of the starfish, gave considerable space to the righting response, but did not touch upon the time-element. Likewise, Hamilton (1922), in a paper devoted entirely to the topic of righting in the starfish, dwelt only on the mechanism of the process, but Fraenkel (1928) furnished some interesting figures on the time it took certain starfish to right themselves. An earlier paper containing time data is the one by Glaser (1907), who studied movements of brittle-stars. Working on the sand-dollar, Parker (1927) made some observations on the time relations of the various phases of righting. His paper also contains numerous references to the literature of body-righting in echinoderms. However, none of the authors mentioned attempted to relate righting-time to temperature, and in the chapter on the echinoderms in *Principles of Animal Behavior* by Maier and Schneirla (1935) there is no mention of a temperature factor in the discussion of righting. Barnes (1937), who lists a great number of biological processes for which temperature characteristics were obtained, has nothing on the subject of body-righting, although he gives several references on the effect of temperature on locomotion, of which, according to Hamilton (1922), the righting of the starfish is one phase.

Methods and Results

In the present investigation recently collected echinoderms were kept in aquaria, with the temperature of the water naturally varying from

18° to 26° C., usually higher in the afternoon than in the morning. The particular specimen to be observed was transferred to a very large Petri dish, filled with sea water whose temperature was regulated by the continual addition of chilled or warmed sea water and gentle stirring, thus maintaining the selected temperature within one-half a degree C. The animal was allowed to remain in the warmed or cooled water for at least 15 minutes, and, judging by its behavior, it acquired the temperature of the new medium during that period. The procedure followed was to lift the animal in the water and lay it in the upside-down position, as symmetrically as possible, on the bottom of the dish. The righting was observed both from above and from the side.

In general, no righting response could be elicited below 10° C. and above 30° C., and most of the observations were made at temperatures varying from 14° to 26° C. As a rule, 10 to 20 trials were made at one temperature level, then the water warmed or cooled, and another series of tests made at the new temperature level. In some cases the righting-times at half a dozen different temperatures were determined in succession, and the same animal observed again later in the day, or after an interval of several days. The righting-time was measured by means of a stop-watch, and in most cases the time required to turn through an angle of 90°, as well as the total turning-over time, was noted.

Sea-urchins

These animals usually turned over in $1\frac{1}{2}$ -2 minutes, with the greater portion of the period (71-95 per cent) needed for the first 90°. Sometimes, after turning through an angle of 130-150°, the animal would fall with a thud, apparently of its own weight. At low temperatures, however, sea-urchins often failed to complete the righting, remaining at an angle of 30-40° to the horizontal for a long time. On the other hand, at high temperatures the animals were likely to remain in the dorsal position, continuously executing translational or rotational movements (about a vertical axis). At 15° C. it took, on the average, $3\frac{1}{2}$ minutes for a sea-urchin to turn over, and the best performance was at 24-26° C., when the mean total righting time was about 80 seconds, with the first half of the turn carried out in 66 seconds. The disparity between the fractions of the total righting time taken to turn through the first, as compared to the second 90° was greater at lower than at higher temperatures.

There was no evidence of fatigue on subjecting the sea-urchins to repeated righting. For example, mean figures in seconds for successive series of ten trials in different specimens were 77 and 75, 83 and 93, 83 and 79. Figure 1*a* shows the relation between the reciprocal of the

absolute temperature of the water and the logarithm of the speed of righting (reciprocal of the righting time in seconds). Applying the Van't Hoff-Arrhenius equation to the data upon which this figure is based, a temperature characteristic of 19,000 calories was obtained.

Through the courtesy of Professor H. L. Clark, I was able to test the effect of temperature on the righting of three spiny urchins. They

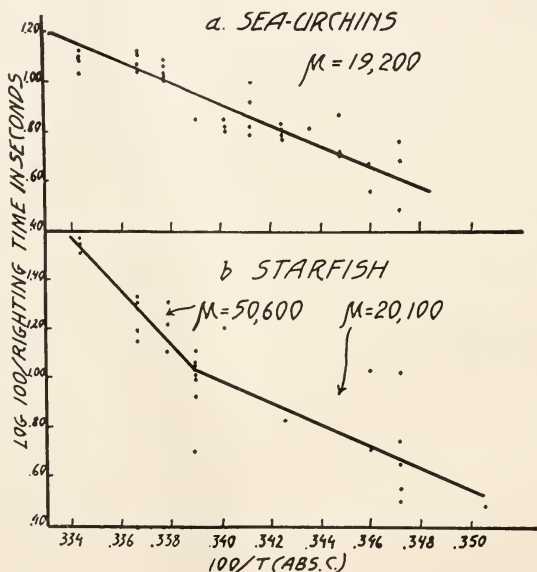


FIG. 1. The relation of the speed of righting, expressed as the logarithm of the reciprocal of the righting time in seconds, to the reciprocal of the absolute temperature of the water: a, for the sea-urchin, *Lytechinus variegatus atlanticus*, with one slope, and b, for the starfish, *Stolasterias tenuispina*, showing a break in slope at 22° C.

behaved in every way like the common sea-urchins, although they depended for their turning on the movements of the large spines, rather than those of tube-feet. Their performance was best at 26° C., when they turned over, on the average, in less than 70 seconds.

Starfish

As already stated, the characteristic features of the righting response of the starfish have been adequately described by Jennings, Hamilton,

and others. Because several arms may participate in the turning process, sometimes interfering with each other, it is much harder than in the case of the sea-urchin to tell exactly when the starfish is half-turned. Therefore a certain position of the upper pole of the animal was accepted as indicating the midpoint of the response. Furthermore, as the arms often became entangled, the completion of the righting was also judged by the position of the upper pole, rather than the complete spread of the several arms.

At 6° C. the animals did not move at all, when in the upright position, and one arm was usually characteristically twisted and curled. Between 8° and 10° C. they would begin to stir, but did not crawl. Above 11° C. it was possible to obtain a righting response, first in 10–15 minutes, then in less time as the temperature was raised. As in the case of the sea-urchins, it took the starfish 66–93 per cent of the total righting time to execute the first half of the turn, and also as with the sea-urchins, the disparity between the fractions of time required to turn through the first and second 90° was greater at lower than at higher temperatures. The optimum temperature was 26° C., when the righting time was, on the average, 27 seconds. This figure compares well with the figures of Fraenkel (1928) for the righting time of “fast” starfish as 25 to 50 seconds, and of “slow” animals as one to three minutes.

Unlike the sea-urchins, the starfish showed evidence of some fatigue. One animal, kept at 21° C., gave the following figures, in seconds, for turning over, in two successive series of ten trials each: 41 to 60 and 54 to 122; another animal, at 23° C., showed a variation of from 55 to 89 seconds for the first ten trials, and 85 to 120 for the next. There was also a greater day-to-day fluctuation in the righting time of a particular starfish, at a certain temperature level, than there was in the sea-urchins. This resulted in a greater scatter of temperature-righting-time data, as plotted in Fig. 1*b*, but it is possible to discern two distinct trends in the curve, with a break at 22° C., and a temperature characteristic of about 20,000 cal. at lower temperatures and one of 50,000 cal. at higher.

Brittle-stars

These animals made no attempts to turn over at temperatures below 10° C., although the arms would execute undulating movements, and some could move short distances while in the dorsal position. At 14–15° C., they often required from 5 to 10 minutes to right themselves, thus not differing greatly from sea-urchins and starfish. At higher temperatures, however, they responded with great rapidity, their best time being only 5–6 seconds. On the other hand, brittle stars tired very quickly, first showing a marked lengthening of the righting time, then

failing to respond altogether. For example, mean figures in seconds for successive series of ten trials on one animal at 22° C. were: 13, 22, 29, and in the fourth series only two responses of 27 and 53 were obtained, before the animal stopped responding to being placed on its back. Similar results were reported for brittle-stars by Glaser (1907), with the best righting times of only 3-4 seconds and rapid fatigue in some, though not in all animals tested.

The variability of the data as well as the fatigability of the animals resulted in such a scatter of the temperature-righting-time figures as to make it impossible to calculate a temperature characteristic of the process.

Discussion

The application of the Arrhenius equation to the relationship between the rate of biological processes and environmental temperatures has been confined mainly to such activities as enzyme action, oxygen consumption, carbon dioxide assimilation, embryological development, or to such organ and tissue performances as breathing, heart rate, nerve and muscle physiology. The only neuromuscular activities involving the organism as a whole to which this equation has been applied were locomotion, as cited by Barnes (1937), and reaction time of the human subject, as reported by Kleitman, Titelbaum and Feiveson (1938). In this investigation it was found that such a global process as body-righting is also subject to the effect of temperature. The echinoderms studied all failed to right themselves below 10-11° C., and at the lowest effective temperatures all took from 5 to 15 minutes to turn over. Although the righting time progressively decreased in all with a rise in temperature and the optimum performance attained in all at the level of 24-26° C., the shortest righting time was quite different for each of the three classes of echinoderms. It was longest (80 seconds) for the sea-urchin in which the process was least complicated, depending as it did on the action of successive groups of tube-feet, brought into play as the animal was turning over. It was shorter for the starfish (27 seconds), which, although it essentially depended on tube-feet action, had to follow the initiative of one or more of its arms, sometimes several arms working against each other in attempting to turn the animal in opposite directions. It was shortest (5-6 seconds) for the brittle-star that performed the righting by muscular action entirely.

On repeated testing the slowest of the three, the sea-urchin, showed practically no fatigue; the fastest, the brittle-star, tired very quickly; while the starfish, in this respect, too, occupied a middle position. Whether the ultimate failure to turn over was due to fatigue of the receptor or central nervous mechanism has not been established.

Concerning the temperature characteristics, it will be recalled that the righting of the sea-urchin had one μ value of 19,000, while that of the starfish had two: 20,000 below 22° C. and 50,000 above that temperature. Barnes (1937) states that when there is a break in the slope of the rectilinear relation between the logarithm of the rate of activity and the reciprocal of the absolute temperature, the μ values in the higher temperature range are usually smaller than those pertaining to lower temperatures. In the righting of the starfish the reverse was true, but there have been reports of many other biological processes with a greater μ value at higher temperatures, among them such a global activity as locomotion of the ant, studied by Barnes and Kohn (1932). Although it was impossible to obtain a definite μ value for the righting of the brittle-star, the available data suggest a high μ value at the upper temperature levels.

It may be added that, in taking 66-93 per cent of the total righting time to turn through the first 90°, the sea-urchins and starfish behaved like the sand-dollars studied by Parker (1927), who found that "the lift from the horizontal to the vertical requires as much as 3 hrs.; the drop from the vertical to the horizontal about half an hour." The similarity is particularly striking in that the sea-urchins and starfish turned in water and their total righting times were expressed in minutes or seconds, while the sand-dollars partly buried themselves in sand and took several hours to turn over.

Summary

The speed of a global activity of three echinoderms, in the form of body-righting, is related to their temperature, within the physiological limits of 10° to 30° C. The speed increases as the temperature rises, and optimum performance is obtained at 24-26° C.

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